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On atavistic Variation in Oenothera cruciata

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After *Oenothera Lamarckiana* had shown itself to be a very proper material for the study of the mutations by which new species suddenly arise from old ones, I was naturally led to investigate whether in other plants similar mutations might not be met with. For it is clear that the phenomena shown by Lamarck's evening primrose are of prevailing interest only if they may be taken as an instance of a general rule. The other species of the same genus were of course the first to receive attention. Most of these showed no signs of being fit for a study along the same lines, while on the other hand one, *Oenothera cruciata*, was found to be inconstant in the very character to which it owes its name. At least the plant which is cultivated under this name in European botanical gardens is variable in this regard.

In proposing to bring the results of my experimental cultures of this plant before the readers of this journal, my aim is principally to direct their attention to any deviations which the species of the above-named genus might show in their native localities. For it is of undoubted interest to the study of mutability to know whether the variability which *Oenothera cruciata* displays with us is also met with in America, in those parts where the plant grows wild. The allied forms such as *O. biennis* and *O. muricata*, should be tested in the same direction. Any deviations from the original types should be carefully observed and if possible perpetuated by seeds. Wherever such deviations are found the question would have to be answered whether the general type of the locality possesses the power of again producing this deviation, and perhaps others too, in succeeding years.

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Oenothera cruciata Nutt. or *Onagra cruciata* (Nutt.) Small, as it is also called, has been described and figured in Britton and Brown's "Illustrated Flora of the Northern United States, Canada and the British Possessions" (2 : 485. 1897). It is a rare plant, found wild from Vermont to New York and Massachusetts, and ascends to 2,000 feet in the Adirondacks. It is described as being annual and flowering from August to October. It may readily be recognized, even without flowers, by the narrowly oblong or oblanceolate leaves and the purple color of the nerves and the stem. The flowers are as small as those of *O. muricata*, but the spikes are much more slender and the fruits are less broad. In all these characters the European plants correspond exactly with the description given by Britton and Brown. The petals of the American type are linear instead of being broad and obcordate as in the allied species.

As yet I have not had an opportunity to cultivate the original wild species, but I hope to be able to do so next year, as I have obtained seeds from the Adirondacks through the kindness of Dr. D. T. MacDougal, of New York, and Dr. B. L. Robinson, of Cambridge, Mass.*

Dr. MacDougal had also the kindness to ask Dr. Britton about an eventual variability of the petals, but the celebrated author of the Illustrated Flora informed him that *Oenothera cruciata does not make broad petals* in America.

This is the essential point. For in all the cultures I have as yet been able to make from seeds of this species, sent to me from different botanical gardens in Europe, I found the form of the petals to be varying in a high degree, so as to reach, in many individuals, the same outline as is presented by the petals of the allied species, *O. biennis*, *O. muricata* and others.

For this reason, I presume that our plants are not the typical *O. cruciata* of Nuttall, but a variety, which perhaps has been produced from it in Europe. Therefore I have called my plants *O. cruciata varia*, merely in order to distinguish them from the pure species. How this variety may have originated of course I do not know. Two possibilities present themselves. The one is by mu-

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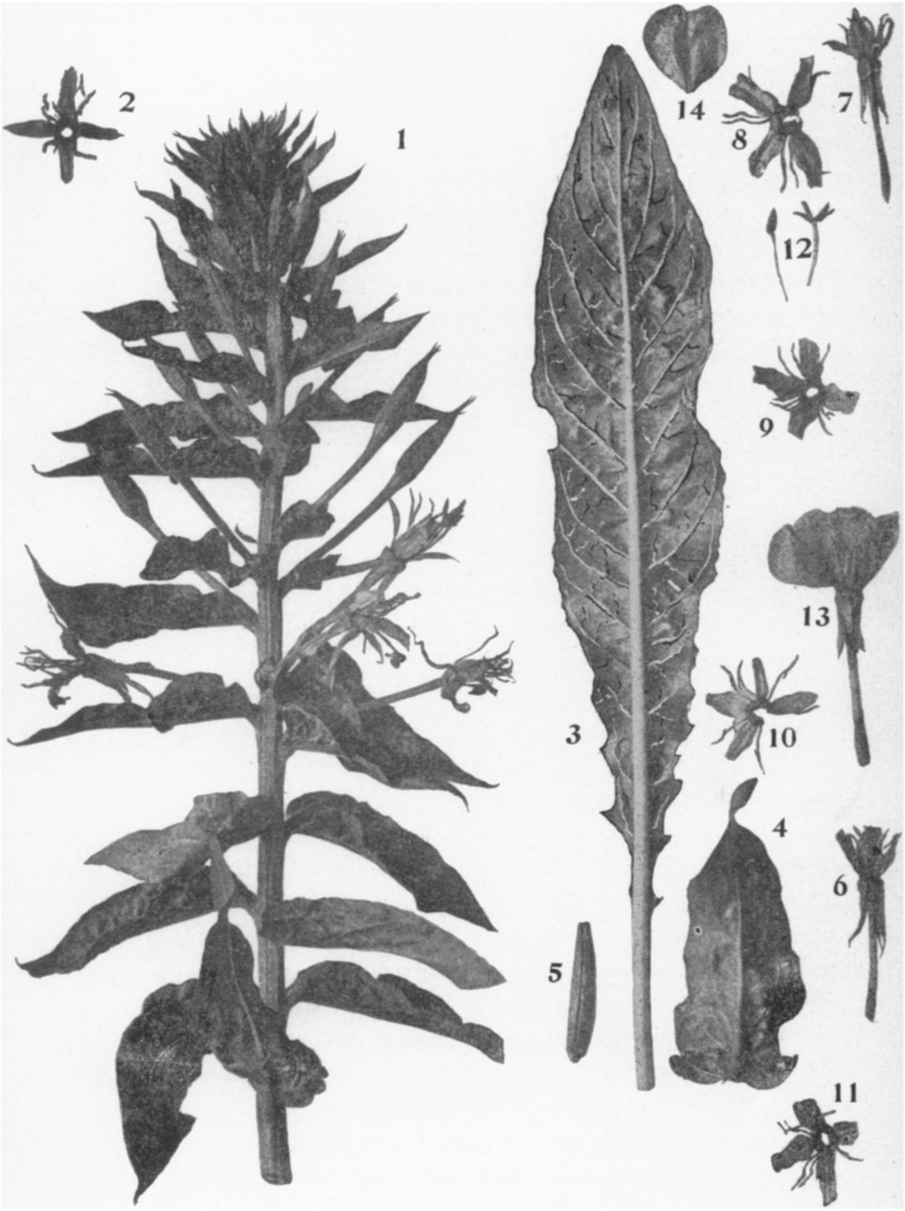
* Seeds from different localities would be always very welcome to me, as the plant may be in a mutable state in some districts, while it is not so in others.



Figs. 1, 2. *Oenothera cruciata* Nutt.
Figs. 3–14. *Oenothera cruciata varia* De Vries.

tation, in the same way as many of our ordinary varieties of garden plants have been produced, the other is by crossing, which is perhaps a still more common source of new garden varieties.

Both possibilities seem to me to be of some interest, since they bear directly on the great question of the internal causes of inconstancy in general. For in my variety the petals do not vary according to Quetelet's law, about a mean, which lies somewhere between the obcordate and the linear form, producing petals of which the majority do not essentially differ from this mean, whilst the extremes are very rare. Quite on the contrary, the obcordate and the linear petals seem to be two alternating types only united by rare intermediate steps.

In case my variety originated by a mutation, we would therefore have an imperfect one, producing the new type only in part of the individuals and remaining true or returning to the pure form of *Oenothera cruciata* in the others. In many points this case would be analogous to that of *Oenothera scintillans*, which originated in my garden from *O. Lamarckiana*, but which, though artificially pollinated with its own pollen, returns in each generation in often a relatively large part of the individuals to the original type.

In case my variety originated by a cross, it should first be remarked that the supposed hybrid is not intermediate between *O. cruciata* and some allied species, but that it has, as far as I can judge, all the characters of the former, the constancy in the form of the petals excepted. I have endeavored to show in my "Mutations-theorie" (Part II., p. 100) that *O. muricata* is probably the only species which could have given such a hybrid with the *O. cruciata*. Now it is clear that having once obtained seeds from the original and constant *O. cruciata*, I possess the materials to bring about this crossing and also those with other allied species, and to try whether it will be possible to get an inconstant hybrid in this way. I propose to do so, but from what I know of my *O. cruciata varia* and of the hybrids I have made of it with more than one other species, it is very improbable that the hybrid *O. cruciata* × *O. muricata* will be as a rule inconstant. It is far more probable that it will exhibit the dominant character, which must be the broad petals, and either give a constant progeny with this feature or split up according to Mendel's laws. I take the broad petals to be phylogenetically older than the linear ones, because they are the rule in the whole genus. But some authors suppose that from time to time there arise exceptions to the ordinary laws governing hybrids, and that such exceptions might be the source of many inconstant varieties and even of inconstancy in general. In this case the chance of getting such an exception by crossing would scarcely be greater than that of getting a mutation from the pure type.

However slight these chances may be, I propose to try both ways and to see whether it would be possible to repeat the as yet doubtful and unknown original production of my *O. cruciata varia.* For there are not a great many cases in which the starting-points are to be had in so pure and so thoroughly controlled a state as in this instance. As to the question of the rule of the constancy of *O. cruciata* under cultivation, and of the hybrids, I hope to solve this in some years ; but as to the chances of getting exceptions, it is evident that these are only small and that it would be preferable if the same experiments were made by a number of investigators.

The aim of such experiments would be to repeat artificially the production of *O. cruciata varia* and by this means to throw some light on its origin in particular and on the origin of inconstant varieties in general. With a view to the possible repetition of this cross I will now give a description of the inheritance of the broad and linear petals in this variety. In so doing I limit myself to the detailed exposition of a single experiment carried on with the descendants of one original specimen of my variety.

In the year 1897 this plant was raised from seed obtained in the usual way of exchange between botanical gardens. I obtained but a single specimen, which bore all the characteristics of the typical *O. cruciata.* The spike, before the opening of the flowers, was placed in a bag of prepared parchment paper to prevent any visits from bees. The anthers touch the stigmas when opening, and the flowers fertilize themselves without any aid. In the same way I always took care to collect each year purely pollinated seeds only,

This original plant bore but a few seeds, from which during the next year I obtained only sixteen flowering individuals. But this number was sufficient to show the whole range of the variability of the race. Nine plants bore typical cruciate flowers with linear petals, two specimens had broad obcordate petals like those of *O. muricata*, and the five remaining had an intermediate breadth, varying in all degrees between these two extremes. Even on the same spike the petals of the different flowers were in this regard unlike each other, and sometimes of the four petals of one flower some were narrow and others broad. I also found petals large on one side of the median nerve and small on the other side.

I obtained pure seed of some of the narrow-petalled ones and of some of the intermediate specimens, separately for each plant, and the next year (1899) had four groups flowering. Two of them from two typically cruciate mothers repeated this type only, each group in thirty plants. One group, also from a cruciate mother, produced twenty-two typical and eight atavistic individuals, meaning thereby those with broad obcordate petals. Intermediate types were wanting. So it was with the fourth group, the children of an intermediate mother, of which only four were purely cruciate, the remaining fifty-eight being atavistic.

Afterwards I continued these four strains, sowing from the two last named in 1900, from the first named in 1901. The atavistic mothers gave only children which were in this regard like them. The purely cruciate strains on the other hand continued to produce atavistic and intermediate types, and these last were also inconstant as far as I observed them.

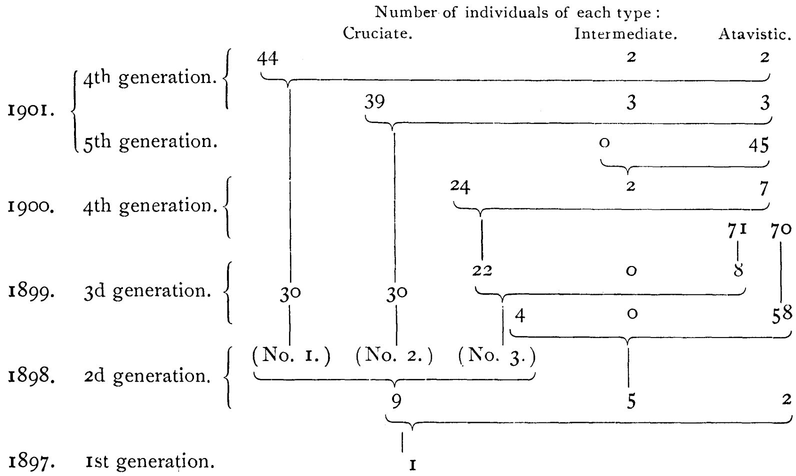
Taking the five generations together, I had 232 children from cruciate mothers, 103 from intermediate and 141 from atavistic parents. The first group consisted of 85 per cent. cruciate, 5 per cent. intermediate and 10 per cent. atavistic individuals. The second, of 4 per cent. cruciate, no intermediate and 96 per cent. atavistic specimens. The third was nearly constant, all individuals bearing the broad obcordate petals.

I say nearly constant, for among those atavists I observed some cases of bud-variation, by which they returned to the cruciate type. This rare phenomenon occasionally presents itself without apparent reason, but it may be induced to appear oftener in the following manner. Around the main stem the plants produce a circle of smaller stems growing upwards from the axils of the root leaves. In my cultures these side-stems do not ordinarily become tall enough to bear flowers. But by cutting out the main stem at an early period I could induce the others to a more vigorous growth. I repeatedly made this experiment; but will only cite here observations made on a single plant in the summer of 1901, grown from seed of a purely cruciate parent. It made six side-stems, out of which three bore only atavistic or broad-petalled flowers. The three other stems likewise produced obcordate petals, but not exclusively, bearing on one side of the spike flowers with the narrow and variable petals of the above-named intermediate types.

Such cases prove that the atavistic individuals are not, or at least are not always, so constant as could be deduced from the figures above given. Analogous instances of sectorial variation, one sector of the spike bearing other flowers than the remaining sectors, were from time to time observed on atavistic individuals and also on intermediate ones, the sport giving flowers with obcordate petals. As yet I have found no such sports on plants of the purely cruciate type nor purely cruciate flowers on those of the two other types. But I have no doubt that this is only due to the small extent of my cultures.

PEDIGREE OF

Oenothera cruciata varia



I give, above, the description of my whole race in the form of a pedigree, omitting the sectorial and bud-variations, again reminding the reader that in every case the seed-bearing plants were fertilized only with their own pollen after enclosure in bags of prepared parchment-paper.

Though the figures of this experiment are but small, they seem to be sufficient to prove the presence of a very curious case of variability, the alternation between the typical cruciate flowers of the species and the atavistic petals of the group to which the species belongs, and to justify the provisional name chosen for my race : *Oenothera* or *Onagra cruciata varia.*

AMSTERDAM.